

## VARIATION AND ADAPTATION IN THE IMPORTED FIRE ANT

EDWARD O. WILSON

University of Alabama

W.L. Brown, Jr.  
COLLECTION

Received August 28, 1950

### INTRODUCTION

The South American fire ant *Solenopsis saevissima richteri* Forel is one of the insect pests which has become recently established in the Southeastern United States. In 1949 it was reported from Florida, Alabama, and Mississippi (Wilson and Eads, 1949). Its known distribution in these three states at that time is shown in Figure 1. Many other populations have been found during 1950 in Louisiana, Mississippi, Alabama, and Georgia by members of the Federal Bureau of Entomology and Plant Quarantine stationed at Mobile, Alabama (*in litt.*); these are mostly very young and limited to nurseries which receive shipments of plants from the Mobile area.

The first published record of this ant in the United States was made by W. S. Creighton (1930), who found it initially in urban Mobile in 1925. Creighton was told by H. P. Loding, a local and reliable amateur naturalist, that the ant had first appeared in the bayfront area of Mobile around 1918, had been pushed north of the city by the subsequently invading Argentine ant, *Iridomyrmex humilis*, and had later re-entered its original range. As late as 1928 Creighton found *richteri* still "confined to a comparatively small area extending from the northwestern part of the town to Spring Hill" (*in litt.*). In 1932 L. C. Murphree, scouting Argentine ants in Alabama, recorded *richteri* from several localities in Mobile and Baldwin Counties, including Whistler, St. Elmo, and Fairhope (Murphree, 1947).

The first comprehensive study of this ant was undertaken during the period of March to July, 1949, by Wilson and Eads (1949) under the auspices of the Alabama

State Department of Conservation. The ant was shown to be a versatile but erratic pest, doing extensive damage to seeds and young seedlings of a variety of crops. Part of the data used in the following study was presented in that report. The U. S. Department of Agriculture initiated its own study in July, 1949, and has continued it up to the time of this writing (August, 1950).

During the spring survey of 1949 there was observed an unusual amount of variability in color from nest to nest. This variation included one extreme blackish phase referable to the typical subspecies *richteri*, one extreme reddish phase referable to no described form, and intermediates between the two. Furthermore, the phase referable to *richteri* appeared to be mostly limited to part of the periphery of the range (see fig. 4). Since Creighton in 1930 described the forms he found in Mobile as typical *richteri* and has later stated (*in litt.*) that this form was the predominant one during that early period, the possibility of the present predominance of the extreme reddish phase representing an important change in the population must be considered. The following report is an attempt to analyze and explain the variation in this light from the point of view of the entire population.

Most of the field data presented in this report was obtained during the 1949 survey. Experiments with living colonies and morphological studies were conducted during the following year at the University of Alabama.

Grateful acknowledgment is made to Mr. J. H. Eads for his invaluable collaboration in the first survey of the ant, to Dr. R. L. Chermock for continuous

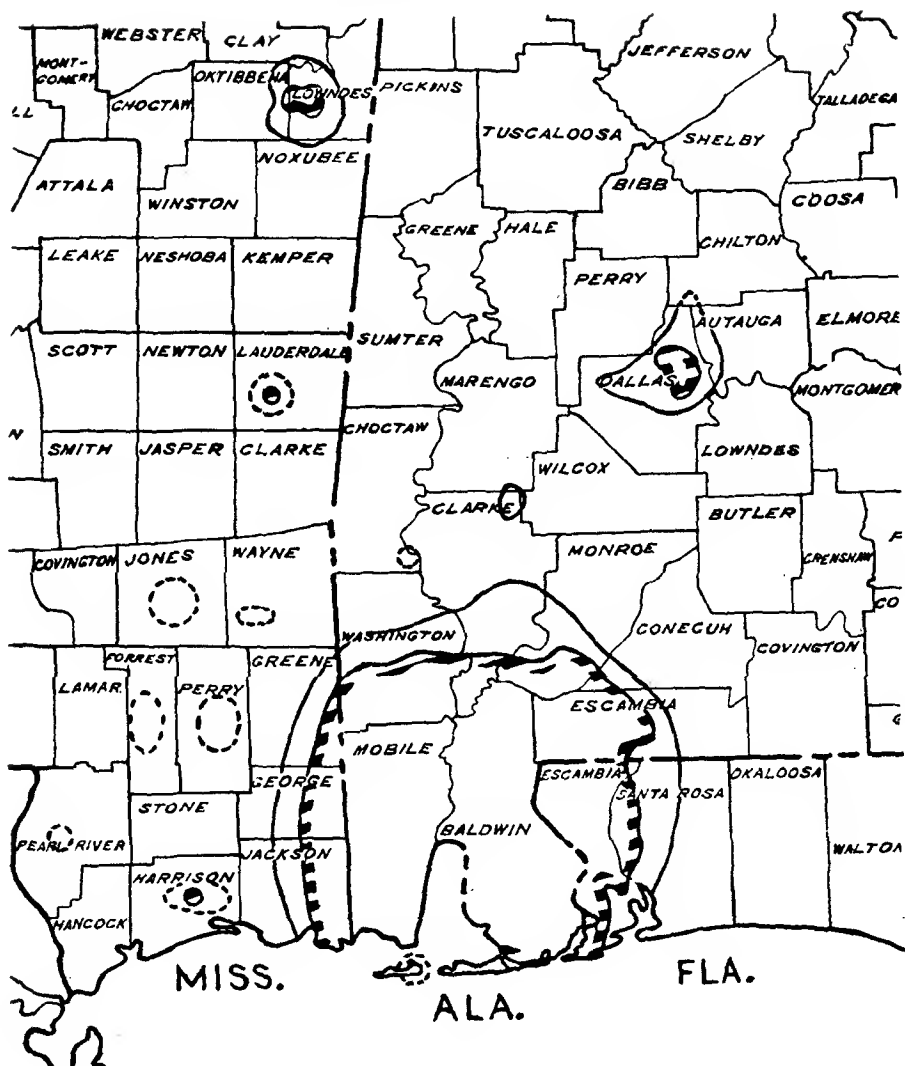


FIG. 1. Known range of the imported fire ant in the Gulf States in 1949. Inner barred lines enclose areas of heavy infestation; outer unbarred lines enclose the extreme range. Dotted circles indicate small populations the ranges of which were not accurately determined. The Choctaw County population and the populations in southern Mississippi were reported by the Federal survey crew (*in litt.*, 1949).

assistance and advice, and to Dr. W. S. Creighton for the hitherto unpublished information concerning the early infestation.

#### STUDY OF THE VARIATION

*Solenopsis saevissima richteri* Forel, as defined by W. S. Creighton in 1930, is apparently the southernmost race of a

highly variable South American ant. Creighton described its range as extending from Uruguay south to the state of Rio Negro in Argentina, west to the Andes, and northwest almost to Bolivia. Another form, *S. saevissima* var. *quincucuspis* Forel, is found over part of the range of *richteri* in eastern Argentina, but it has been distinguished from *rich-*

*teri* only on the basis of a highly variable color character and its validity is very questionable. *Solenopsis s. saevissima* (F. Smith), the typical subspecies, ranges with no great variability from the Guianas to the southern part of the state of Minas Geraes, Brazil. A vast zone of intergradation, containing a complexity of described forms, extends from Minas Geraes west through Bolivia to the Andes, south to Uruguay in the east, and south to the oases area of Argentina in the west. The taxonomic picture here is a very confused one; further study will probably reveal some of the forms to be intergrades of *saevissima* and *richteri*, while some may be shown to represent distinct species. A thorough discussion of the diagnostic characters and the known ranges of these forms has been presented by Creighton (1930). The extreme reddish phase, which plays so important a role in the Gulf States population, has not been formally described from South America, but it is possible that it exists there as a submerged element (see Discussion). The whole Gulf States population has been referred to in this report as *Solenopsis saevissima richteri* strictly as a matter of convenience. This has been its popular designation in reports and correspondence up to the present time. For reasons discussed later it is believed that the new form should not be given immediate formal taxonomic recognition.

The population found in the Gulf States exhibits a great deal of variation. In order to facilitate a more exact study, the extreme variants and their intermediates were divided into six arbitrary phases according to the color of the workers. These can be described as follows:

1. *Extreme dark*. Ground color of alitrunk and head piceous brown; a light brownish orange to light brownish fulvous stripe covering approximately the anterior three-fifths to four-fifths of the dorsum of the first gastric segment in all but the minimas and smallest medias; a similar stripe on the venter of the first gastric segment but the rest of the gaster

piceous brown, the condition seen in all the phases. This is the form best referable to Forel's description of *richteri*.

2. *Dark intermediate*. Ground color of alitrunk and head dark brown but not piceous, and with no reddish tinge evident; stripe on dorsum of gaster similar to above.

3. *Intermediate*. Ground color dark reddish brown, lighter than dark intermediate phase and approximately intermediate between the two extreme phases; stripe on dorsum of gaster similar to two darker phases.

4. *Light intermediate*. Ground color medium reddish brown; stripe on gaster covering approximately one-half to two-thirds of the anterior surface, darker than in above phases, posterior border frequently indistinct.

5. *Dark red*. Ground color light reddish brown; stripe on dorsum of gaster covering approximately the same area as in light intermediate phase but darker, being very close to the color of the head and alitrunk and distinguishable only in contrast to the piceous brown of the rest of the gaster, its posterior border indistinct; stripe present only in larger medias and soldiers.

6. *Light red*. Ground color light reddish brown; stripe on gaster absent or present only in largest soldiers, very similar when present to that of dark red phase.

During the survey three colonies were found which could not correctly be assigned to any of the above phases. One of these, found near Gulf Shores, Baldwin Co., Ala., had workers with the ground color of the dark intermediate phase but with little or no gastric stripe. These are referable to Creighton's definition of *Solenopsis saevissima* var. *quinquecuspis* Forel (1930). The other two, found near Gulf Shores and Fairhope, Baldwin Co., Ala., had workers all of which possessed very nearly the same color as callows of the light red phase.

The queens of all the phases are very similar in coloration to the largest work-

ers and exhibit the same variation. The males are all uniformly black.

Morphological studies of the six phases revealed significant differences only in size. It was found that in workers, queens, and males, the darker phases are larger on the average than the lighter phases. As demonstrated in figures 2 and 3, the successive intermediates tend to show successive differences in size, this being particularly pronounced in the worker caste. All the measurements shown were made of the alitrunk as seen in profile; from the dorsal base of the pronotal collar to the dorsum of the junction of the propodeum and petiole. The alitrunk was used because of its rigidity and the ease with which it is measured. To correlate the variability of the head with that of the alitrunk, the heads in addition to the alitrunks of fifty light red workers and fifty extreme dark and dark intermediate workers were measured in profile from the base of the clypeal spines to the extreme occipital border. No significant divergence was noted in the two sets of measurements nor could the two groups of ants be separated on the basis of head-alitrunk proportion.

In nearly all the areas where many of the phases were observed together it was noted that the darker forms tend to build

larger and proportionally taller mounds. Ten mounds each of light red and extreme dark-dark intermediate phases were measured in an open field several miles south of Theodore, Mobile Co., Ala., in June, 1949, and the following differences recorded:

*Light red*

The smallest mound had a base diameter of 13" × 13" and a height of 5"; the largest had a base diameter of 24" × 22" and a height of 11". Height varied from 3" to 13". The overall average of the base diameters was approximately 24" × 22" and of the heights, 7".

*Extreme dark and dark intermediate*

The smallest mound had a base diameter of 22" × 20" and a height of 10"; the largest had a base diameter of 39" × 24" and a height of 14". Height varied from 10" to 18". The overall average of the base diameters was approximately 27" × 24" and of the heights, 14".

All of the phases tend to accumulate bits of vegetable detritus, small pieces of charcoal, and small pebbles on the surfaces of their mounds, but this is especially noticeable in the darkest three or

	WORKERS	QUEENS	MALES
EXTREME DARK	1.264	2.682	2.712
DARK INTERMEDIATE	1.236	2.635	
INTERMEDIATE	1.130	2.584	
LIGHT INTERMEDIATE			
DARK RED	1.095	2.499	2.604
LIGHT RED	1.038		

FIG. 2. Means of the lengths in millimeters of the alitrunks of the color phases. For each phase a minimum of one hundred workers, twenty queens, and twenty males collected at two or more localities during at least two seasons were measured. Only statistically significant differences are shown.

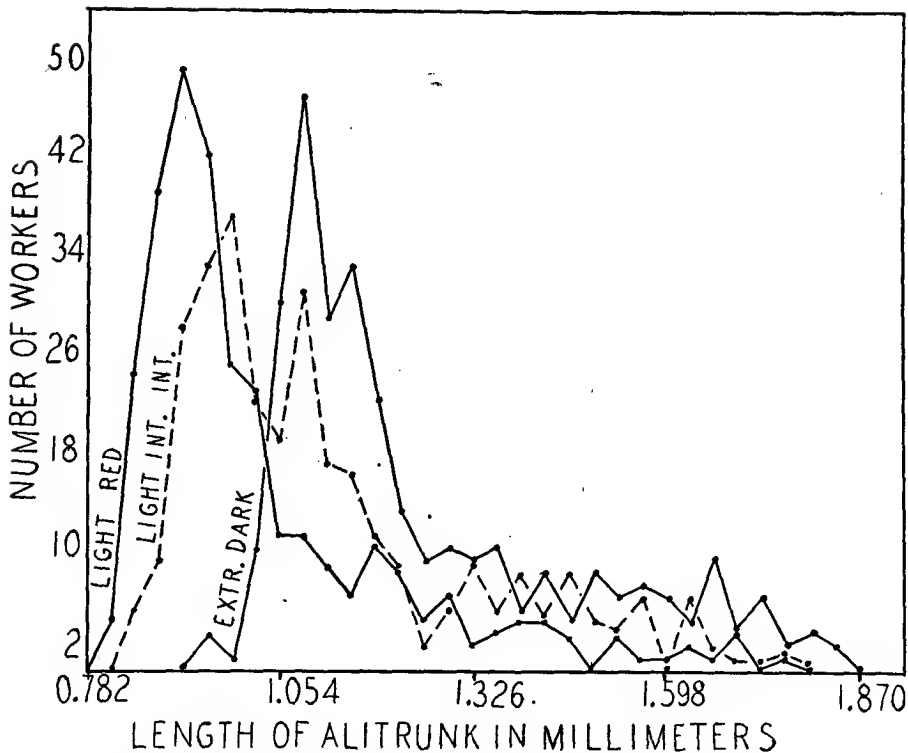


FIG. 3. The distribution of the workers according to size in the two extreme phases and two of the intermediate phases. Three hundred workers from four localities were measured in each group.

four phases. Occasionally mounds of the darkest phases are found nearly covered by a thin layer of this debris. In areas where they occur together it is often possible to tell with reasonable accuracy from a distance which are the darker and which are the lighter phase mounds, judging from the size, shape, and outer surface.

In order to plot the distribution of the color variants 10 colonies each in 84 relatively random localities over the main infested area were classified according to the six color phases. To supplement this a total of 193 colonies were classified in 18 other localities where ten nests could not be found together. Figure 4 shows the approximate distribution of the phases as determined by this survey. It will be noted at once that the darker phases are limited to the southern and eastern portions of the periphery of the range, to

a small part of the western portion of the periphery, and to a number of small, isolated areas throughout the range. It is interesting to add here that the isolated areas are in nearly every case centered around marshy fields or grassland, but not all such situations contain darker phases. The Artesia and Meridian population in Mississippi are apparently homogeneously composed of the darkest one or two phases. In the Selma population the darker phases are scarce and irregularly distributed, and none at all have been found in the Thomasville population. The populations in Louisiana, Georgia, and southern Mississippi have not been carefully classified according to the color phases by the writer. However, Mr. G. H. Culpepper, of the Federal survey crew, has very kindly studied the color variation in these populations and has reported

that with the exception of the one at Meridian all contain a predominance of light phase colonies (*in litt.*). He has expressed the opinion that all but those at Meridian and New Iberia are apparently small and recent in origin.

It is believed that the variation studied in the Gulf States has a genetic basis. This conclusion is based on the following observations:

1. In many areas where both extreme phases and their intermediates occur, colonies of nearly all the phases may be found in the same immediate area, sometimes within a few feet of one another, apparently under nearly identical conditions.

2. Variation within individual colonies is very slight, and in none of the nests examined were there found workers which covered more than two adjacent phases.

3. It would be very difficult to rationalize the distribution of the variants according to environment or colony age. In the main area of infestation the darker forms are mostly limited to the southern and eastern portions of the periphery, while the population at Artesia, in northern Mississippi, is apparently composed entirely of darker forms. The Artesia and Selma populations are both located in the clearly defined "Black Belt," but the Selma population contains very predominantly the two lightest phases.

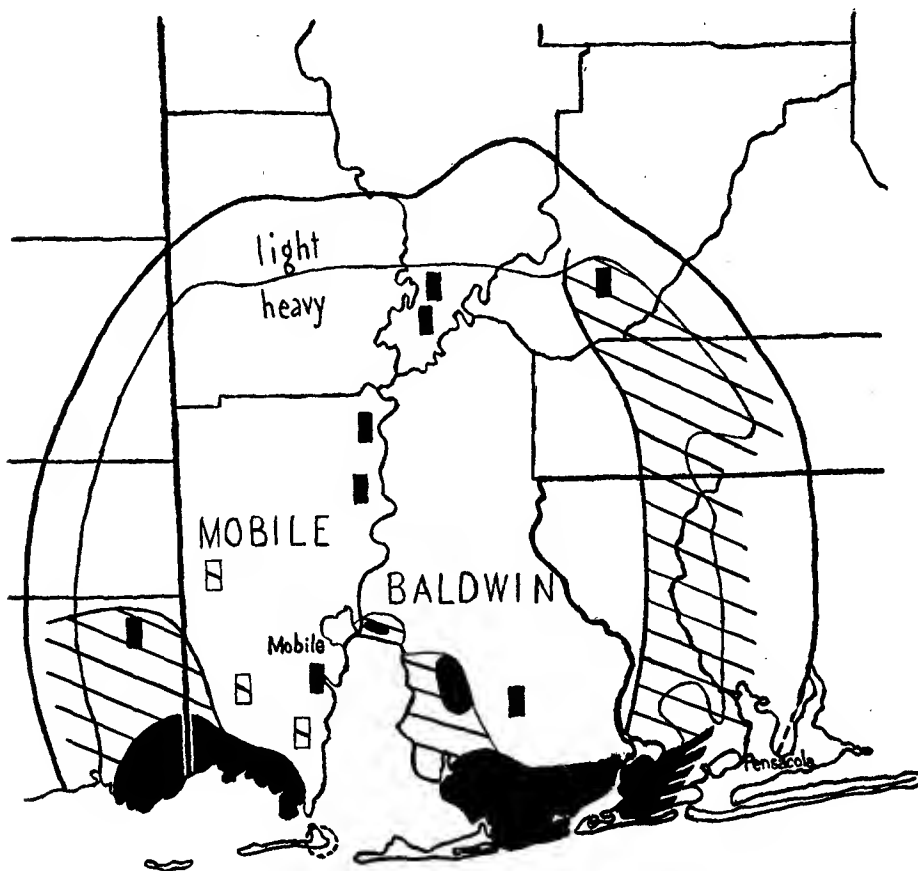


FIG. 4. Distribution of the color phases in the main area of infestation. Intense shading represents areas with incidence of four darkest phases greater than 20 per cent; hatching represents areas with incidence of these phases 5-20 per cent. Small rectangles represent small isolated dark phase populations.

4. Colonies of light red and dark intermediate phases have been maintained in the laboratory under a variety of conditions without appreciable change in the color of the original workers or those reared in artificial nests. Workers have been reared at temperatures above 30° C and below 20° C; others have been heated excessively and chilled. Still others have been reared variously at substarvation and near-optimum conditions. Minima workers of the dark intermediate phase produced under substarvation conditions tend to be lighter in color but are still distinguishable from those of the lightest phases.

5. The brood of two light phase queens adopted by dark intermediate phase workers in the laboratory and one adopted by *Solenopsis geminata* workers developed into workers with the color of their mothers. In each case young, recently fecundated queens were introduced into groups of twenty to thirty workers. These were maintained in Fielde nests modified by the addition of plaster-of-paris chambers and were fed honey, dogfood, and miscellaneous insects. It has been found that occasionally groups of workers, especially those from depauperate colonies, accepted alien queens readily, but in the majority of cases could be induced to do so only after being chilled to immobility from several hours to several days. Many remained hostile regardless of treatment.

#### DISCUSSION

It is apparent that the Gulf States population of *Solenopsis saevissima richteri* has undergone a marked change during the period of 1929 through 1949. The original population was at least mostly composed of the darkest phases, as stated by Creighton. As late as 1929 this remained true (Creighton, 1930 and *in litt.*). In 1932 L. C. Murphree collected the ant from five localities in Mobile and Baldwin Counties, Ala., and judging from his description (1947), the material he collected must be assigned to one or both of the

two darkest phases. In 1941 the writer observed a large number of colonies along the bayfront of urban Mobile and in several areas in the western part of the city, all of which belonged to the lightest two or three phases. By 1949 the darkest phases could be found in some abundance only along part of the periphery in the main area of infestation and even there were outnumbered by the lightest phases. The Selma and Thomasville populations were predominantly light phase, the Meridian and Artesia populations at least predominantly dark.

Two approaches may be used to explain this peculiar recent distribution, one considering the history of the population, the other the possible climatic preferences of the extreme forms. Figure 5 shows the approximate rate and direction of spread of the ant since its introduction, as based on the observations of W. S. Creighton, the records of L. C. Murphree, and the estimates of 65 residents of the main infested area (Wilson and Eads, 1949). It appears that by 1934, while the dark phases may still have been dominant, the ant spread south over the southern portions of Mobile and Baldwin Counties, a range now co-occupied by another introduced ant, *Brachymyrmex heeri obscurior* Forel. Estimates place the origin of the Artesia population around 1935 and the Meridian population around 1940. The Selma population was not in any case estimated to have originated before 1944 nor the Thomasville population before 1948. The light phases were apparently responsible for the ant's explosive spread to the north in the main area of infestation. The partly peripheral distribution of the darkest, presumably oldest phases seems to indicate that they were pushed outward by the expanding light forms, in a pattern somewhat similar to that first demonstrated by Matthew (1939) for the primitive members of some groups of mammals, that is, with the most primitive forms at the periphery and the most recently evolved toward the center. The relatively homogeneous ecologi-

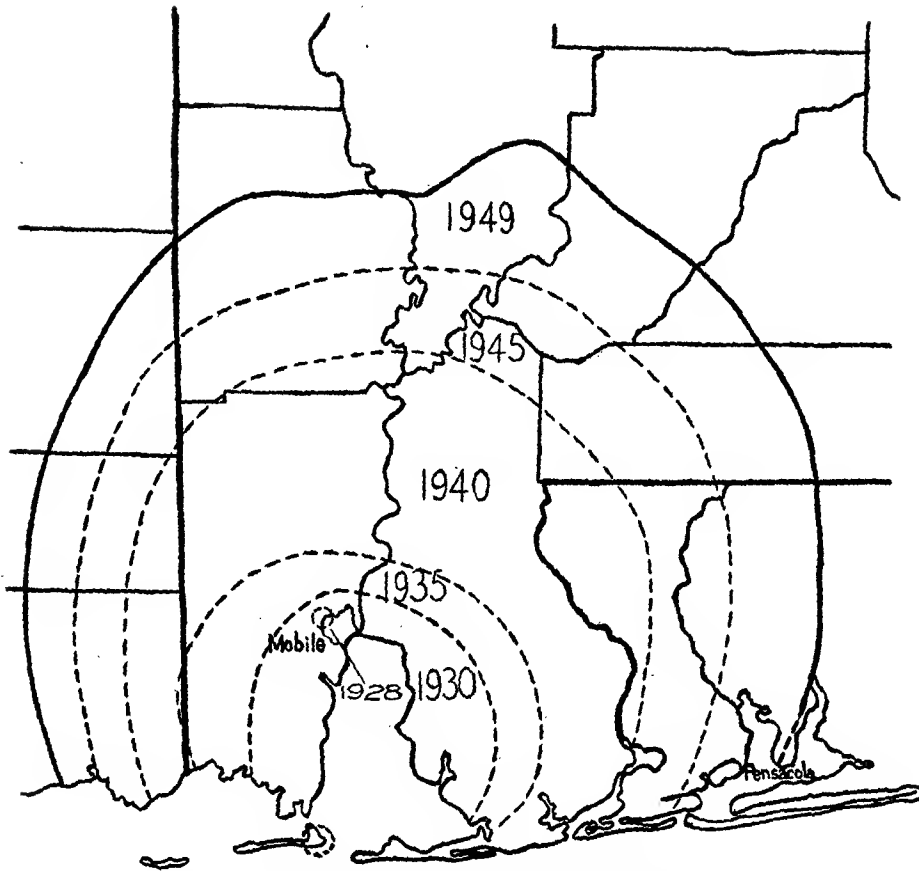


FIG. 5. Estimated rate and direction of spread of the imported fire ant in the main area of infestation.

cal conditions in and around the area of infestation, coupled with the absence of any significant geographical barriers, has allowed an even and steady spread of the ant since its introduction (see fig. 5). It has also resulted in the relatively clear preservation of the concentric pattern produced by the spread of the light forms. The darkest phases were best able to survive along the coast, along the eastern periphery, and in isolated spots through the infested area. Why marshy areas should suit these forms is not known. Large numbers of light phase nests often occur in the same places, with as many as seventy nests to an acre, and competition must be intense. Over much of the southern, continuous part of the range of

the darkest phases, as around Gulf Shores, these forms occur in as wide a variety of situations as the lighter phases. The absence of light phases at Artesia and Meridian might be explained on the basis of early origin, that is, derivation from the early, nearly homogeneous stock. The lack of conspicuous success on the part of these populations, as compared with that of the younger Selma and Thomasville populations, and the southward expansion of the early population in the main area of infestation seem to indicate that the darker phases are poorly adapted to the climate of the Gulf States.

The present predominance of the light phases suggests an adaptive change within the population. The manner by which



these phases have largely replaced the dark phases has been, in the opinion of the writer, partly rapid expansion in range and population size and subsequent dilution of the dark phase genes, resulting in a diversity of intermediate forms; it has also been partly through considerable populational pressure and elimination in direct competition. An indication of this latter process can be seen in the scarcity of dark and intermediate phases over much of the range formally occupied by the dark phases. Another indication can be seen in the scarcity of the native fire ants, *Solenopsis xyloni* and *S. geminata*, and of the Florida harvesting ant, *Pogonomyrmex badius*, in the infested areas. Colonies of the imported fire ant are extremely antagonistic to these ants as well as to alien colonies of their own species. During the survey no colonies of *Solenopsis xyloni* and very few of *S. geminata* were found in the heavily infested areas. *Pogonomyrmex badius* was more common but quite sporadic in distribution. These three species reach relative abundance around the periphery of the imported fire ant's range. Another important consideration in this light is the incidence of the phases. Although exactly random samples in quadrats were not taken during the survey, approximately twice as many nests of the two darker phases were found as those of the two intermediate phases in the counts taken. Assuming that the phases represent nearly equal arbitrary divisions of the successive genotypes, it is possible that this difference in incidence is a result of replacement by the light forms through direct competition as opposed to genetic dilution. The relative importance of these two modes of replacement can only be estimated on the basis of available data, but it seems safe to say that both play an important role.

When considering the significance of the light phases as an adaptive replacement, the possible role of the Argentine ant, *Iridomyrmex humilis* (Mayr), must be studied. This ant reached its peak in

the latter part of the 1920's and during that time succeeded in eliminating nearly all of the native ants in the Mobile area (Creighton, 1950). By 1932 it had been partly controlled and the native ants had begun to infiltrate the infested area. It was this time also that *Solenopsis saevissima richteri* began its initial spread to the south. It would seem quite possible that the decline of the Argentine ant, and not the replacement of the dark phases by the light phases, was responsible for the fire ant's rapid spread to pest proportions. However, several observations have been made which seem to indicate that the Argentine ant had a minor influence on the phenomenon under consideration. One is that the Argentine ant appears to offer the imported fire ant little serious competition at the present time, even in areas where the former are abundant enough to affect the native ants (Wilson and Eads, 1949). The two species thrive together in some areas of Mobile. Another is that the Argentine ant is primarily an urban dweller; it never was able to blanket the wide variety of rural situations in which the imported fire ant thrives (*Ibid.*). There is no reason why the fire ant could not have spread by way of these situations, even assuming that the Argentine ant was able to hamper it during that ant's peak. Finally, the predominantly dark phase *Artesia* population and the predominantly light phase *Selma* population can be critically compared, since both are under very similar conditions. The latter is less than half as old as the former and yet much larger and denser. Both are situated mostly in rural areas, and neither could have been greatly affected by the Argentine ant since their inception.

In considering the possible genetic basis of the variation, there are several peculiarities in the expression of the characters which deserve mention. One of these is the small amount of variability observed in intergrade colonies. This, coupled with the great variability existing from nest to nest, cannot be explained on

the basis of a single mutation. Admitting that the phases are totally arbitrary, that they overlap, and that occasional individuals can be assigned to an adjacent phase, at least four or five distinct genetic groups clearly exist; the workers of the six phases can be divided on the basis of size into five statistically significant units (fig. 2). Part of the difficulties are removed by explaining the variation on the basis of multiple factors or multiple alleles, which could control successional variation of the type observed. Of these two possibilities, multiple alleles seems to be the more tenable. From only three alleles a total of six combinations, or genotypes, is possible. Also, the greatest number of genotypes which could be produced by a single cross is three; the small amount of variability in single colonies studied in the field may well indicate such a limited number of genotypes. On the other hand, a dihybrid cross involving multiple factors showing no dominance would make possible nine genotypes and phenotypes, all of which, including the extremes, could be produced by a single heterozygous cross.

The close correlation between color and size variation and the present selective advantage the light phases hold seems to indicate a pleiotropic expression of whatever alleles are involved, producing a relatively clear-cut combination of characters for both extreme color forms. It would seem unlikely that these combinations of characters could maintain their identity in the extensive intergradation that has occurred unless they were very closely linked.

Even assuming multiple factors or multiple alleles, the small amount of variability within individual colonies is difficult to explain by the familiar laws of heredity. Provided that the queen is heterozygous and diploid, it would seem that the phenotypes of workers produced by an intermediate queen would be mixed according to random assortment. It appears very likely that the reason why this fails to occur in the imported fire ant (and in

many other species of ants which exhibit the same peculiarity in their color varieties) entails an aberrant hereditary mechanism. One such possible mechanism is maternal determinism, a condition demonstrated in the snail *Limnaea peregra* by Diver, Boycott, and Garstang (1925). In this organism the direction of spiraling in the shell is determined by the genotype of the mother, regardless of the genotype of the offspring. On the other hand, in *Solenopsis* a mechanism involving haploidy in the queen and parthenogenesis is apparently rendered untenable, because unfertilized eggs are capable of developing at the most only to the late larval or pupal stage. Mature larvae were noted in fourteen out of fourteen nests containing only young alate queens; one of these nests produced several worker pupae, but since there was no absolute proof that all the queens were not fertilized, general conclusions concerning thelytoky should be avoided. One nest containing alate queens raised from larvae in the absence of males produced only larvae over a long period of time. This was noted in fourteen artificial nests out of fourteen which contained only virgin queens; mother queens in other nests kept up a prolific production of workers. Unfortunately, the interesting and significant problem of the genetic basis of the variation will prove to be a very difficult one to solve. For all practical purposes the colony is the individual in the life cycle of the ant, and with present knowledge of caste determination each generation of virgin queens will have to be preceded by hundreds or thousands of workers.

The origin of the light phases is another problem which can only be conjectured on the basis of available data. Three possibilities are treated below.

1. The light phases could have been a submerged recessive element in the genotype of the original invaders. However, this view is considerably weakened by the apparent homogeneity of the Artesia and Meridian populations, which were probably established while the dark phases

were still dominant. Also, the original invaders were probably few in number; it seems unlikely that they could have contained all the variability present today, unless this were to appear conspicuously in the early population.

2. The light phases could have been derived through mutations in the early, dark phase population. This possibility must always be considered, because the population mutation rate has been potentially tremendously high. Even in the early population, each of the many thousands of colonies were producing hundreds to thousands of sexual forms the year round. Today the number of colonies in the main infested area easily numbers into the millions (Wilson and Eads, 1949).

3. The light phases could have been derived from one or more later introductions. Despite the fact that nothing exactly comparable to the light red phase has ever been described, examination of representative material of most of the South American forms of *Solenopsis saevissima* has convinced the writer that the light red phase could have originated anywhere in the great zone of intergradation from southern Brazil to Argentina. Variation in this area is too great and as yet too poorly defined to dismiss the idea that the light phases were derived anywhere but in the Gulf States.

In final analysis the phenomenon can be described as an adaptive replacement, a shift in population dominance from one genetically distinct form (darkest phases, or *richteri* s. str.) to another (lightest phases). At present the population is quite unstable; it cannot be said to have reached an adaptive peak. Although it appears that a complete replacement is under way and a homogeneous population is in the making, new forms such as the two anomalous phases (see discussion of variation) may yet rise to dominance. The origin of the new form is not known. Because of this instability and uncertain origin, it does not seem wise to accord the light phases immediate formal

taxonomic recognition, although by strict definition it might appear to some authorities to constitute a new subspecies. Otherwise, the question of the origin is an academic one only. Whether indigenous or introduced the light phases have functioned as a favorable mutation appearing in the population; they seem to have progressed very much as such a mutation would be expected to progress. As an example of this type of phenomenon the adaptive replacement in the Gulf States population is especially noteworthy. This is due to three significant conditions:

1. The new forms are easily identified and their history and present distribution can be carefully studied because of a distinct color character.

2. The adaptive change within the population has occurred so recently as to aid greatly the study of its history. The new forms constitute an almost vertical evolutionary change which has taken place in less than twenty years. Their history illustrates the extremely rapid rate with which such a change, which can be interpreted as an initial step in subspeciation, can occur in a population of insects. Similar changes have been observed in populations of the scale insects *Aonidiella aurantii*, *Coccus pseudomagnoliarum*, and *Sassia oleae* (Quayle, 1938), and of the codling moth, *Carpocapsa pomonella* (Hough, 1934, and Boyce, 1935).

3. The very uniform terrain of the Gulf Coast area has allowed an identifiable preservation of what is apparently a concentric distribution of the old and new forms. That the dark forms have been pushed out along the periphery is still evident in their distribution today.

This populational change is indicative of the way that evolution can proceed in any population of ants. However, the rapidity with which this has occurred is probably rarely equaled by that in endemic species. Too little is known about North American ants at the present time to determine precisely the rates of evolution, but it appears that most holarctic genera have been evolving at a consid-

erably lower rate than such better known groups of insects as the Rhopalocera. For instance, postglacial relics are rare or absent, and subspeciation initiated by glacial isolation seems to have progressed to a relatively slight degree. The accelerated evolution in the imported fire ant probably has the same origin as the explosive spreads of imported insects as a whole: the removal of the biotic pressures (parasites, competition with other insects, etc.) which controlled it in its native environment. If this is true, then the population change in the imported fire ant can be regarded only as a swiftly enacted replica of the normal evolutionary processes and not as typical subspeciation.

#### SUMMARY

1. The imported fire ant, *Solenopsis saevissima richteri* Forel, is the southernmost race of a widespread and highly variable South American ant. It was introduced into the port of Mobile, Alabama, sometime around 1918 and by 1949 had spread to parts of Florida, Mississippi, and Louisiana.

2. A great deal of color variation from nest to nest has been noted in the Gulf States population. This includes an extreme blackish phase referable to the original description of *richteri*, an extreme reddish phase referable to no described form, and intermediates between the two. This color variation is correlated with differences in size of the ants and in appearance and proportion of their nests.

3. The variation has a genetic basis. It is suggested in this study that the variation can be explained most readily on the basis of multiple pleiotropic alleles.

4. The history of the variation has been determined as follows:

The darkest forms, or *richteri* s. str., were the ones originally dominant from the time of the ant's introduction until at least 1929 and probably sometime after 1932. The origin of the new form is not known, although it is believed that it originated either through mutation within

the population or through a second introduction. In 1949 it was by far the dominant form. It had apparently replaced the typical *richteri* partly by rapid expansion and subsequent genetic dilution and partly through natural selection by direct competition. Its predominance in the main population and in at least two smaller isolated populations has evidently been responsible for a much greater success of the species. In the main population in 1949 the typical *richteri* was mostly limited in distribution to portions of the periphery of the range, forming with the new form roughly the concentric pattern of Matthew's modified Age-and-Area hypothesis.

5. The new form has been interpreted as functioning, regardless of its origin, as a favorable mutation introduced into the population. Its rise to dominance has constituted an extremely rapid, nearly vertical evolutionary change.

#### LITERATURE CITED

- BOYCE, A. M. 1935. The codling moth in Persian walnuts. *J. Econ. Ent.*, 28: 864-873.
- CREIGHTON, W. S. 1930. The new world species of the genus *Solenopsis*. *Proc. Amer. Acad. Arts and Sci.*, 66: 39-151.
- . 1950. The ants of North America. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 104.
- DIVER, C., A. E. BOYCOTT, AND S. GARSTANG. 1925. The inheritance of inverse symmetry in *Linnaea peregra*. *J. Genet.*, 15: 113-200.
- HOUGH, W. 1934. Colorado and Virginia strains of codling moth in relation to their ability to enter sprayed and unsprayed apples. *J. Agric. Res.*, 48: 533-553.
- MATTHEW, W. D. 1939. Climate and evolution. *Special Publications of the New York Academy of Science*, 1: 1-223.
- MURPHREE, L. C. 1947. Alabama ants, description, distribution, and biology, with notes on the control of the most important household species. Unpublished Master's thesis, Mississippi State College.
- QUAYLE, H. J. 1938. The development of resistance in certain scale insects to hydrocyanic acid. *Hilgardia*, 11: 183-225.
- WILSON, E. O., AND J. H. EADS. 1949. A report on the imported fire ant *Solenopsis saevissima* var. *richteri* Forel in Alabama. Special mimeographed report to the Director of the Alabama State Department of Conservation.